DESCRIPTIONS OF THE TYPE-SPECIES OF THE EARTHWORM GENERA PLUTELLUS AND DIGASTER (MEGASCOLECIDAE: OLIGOCHAETA)

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INTRODUCTION

Since Perrier (1873) described the type-species of Plutellus, P. heteroporus, some 104 species from the Australian Region, New Zealand, the Pacific Nearctic, the northern Neotropical and the Oriental Region have been added to the genus. The supposedly Pennsylvanian origin of P. heteroporus has been questioned by Gates (1961). Jamieson (1970 a, 1971) suggested that the type-species was Australian as its morphology was extremely close to that of Plutellus manifestus from New South Wales, the similarity extending to a peculiar alternation of nephropores unknown elsewhere in the Oligochaeta though approached in the Australian genus Heteroporodrilus Jamieson, 1970 a. The morphological heterogeneity and widely disjunct distribution of the genus indicates that the genus will have to be split into several independent and not necessarily closely related genera. Redescription of the type-species is fundamental to revision of the genus and is attempted below.

The genus Digaster was erected by Perrier (1872) for a single species, D. lumbricoides, from the vicinity of Port Macquarie in northern New South Wales. Subsequent additions to the genus were D. armifera Fletcher, 1887, and D. perrieri Fletcher, 1889, both from New South Wales, and seven Queensland species, D. brunneus Spencer, 1900; D. gayndahensis Spencer, 1900; D. lamingtonensis Michaelsen, 1916; D. longmani Boardman, 1932; D. minor Spencer, 1900, and recently D. anomala and D. bradburyi both of Jamieson, 1970 b. A description of an eighth Queensland species from Springbrook is in preparation. Inclusion of these species in the genus as it had been defined by Perrier was indicated by the occurrence of two gizzards with a single pair of combined male and prostatic pores, the prostates being racemose. The genus was extended by Beddard (1895), Sweet (1900) and Jamieson (1963) to include species with three gizzards which had initially been placed in Perissogaster Fletcher, 1887.

Jamieson (1970 b) showed that the Queensland species formed a species-group characterized by presence of gizzards in segments VI and VII and of stomate nephridia median to micromeronephridia in posterior segments. It was suggested that D. lumbricoides also belonged to this group and that the affinities of the group lay with a Digaster-Megascolides group of genera (Jamieson, 1971) by virtue of the condition of the nephridia described above. It

was shown that Perissogaster must be resurrected as the type-species, P. excavata, lacked posterior stomate nephridia as did P. nemoralis. The status of Perissogaster queenslandica requires further elucidation. That the Queensland Digasters were congeneric with D. lumbricoides remained uncertain, however, as Perrier had not described its nephridia and stated that a gizzardless segment intervened between the two segments containing the gizzards. Further uncertainty was introduced into the definition of the genus by doubts expressed by Perrier as to enumeration of segments in the type-specimens. The courtesy of Dr. Renaud-Mornant in permitting the author to examine the type-specimens allows redescription of the morphology and elucidation of the affinities of this species.

Plutellus heteroporus Perrier, 1873 (Fig. 1 A-H)

Plutellus heteroporus Perrier, 1873, pp. 245-268, fig. 1-3. Plutellus heteroporus : Beddard, 1895, p. 487; Michaelsen, 1900, p. 174.

Length?; width (segment 45) = 2.7 mm; number of segments? Pigmentless buff in alcohol. Segments anteriorly simple, becoming triannulate in XX posteriorly. Prostomium damaged but apparently tanylobous as noted by Perrier. First dorsal pore in 7/8 (perforate); a suggestion of a pore (imperforate) at 6/7, in which Perrier observed the first pore. Setae clearly visible, in 8 longitudinal rows throughout, in 11 posteriorly; ab absent, cd present in XVIII.

Table 1

Intersetal distances in segment XII in Plutellus heteroporus

	aa		ab		be		ed		dd		dd : u
	mm	st*	mm	st	mm	st	mm	st	mm — —	st	
intervals/ab						13.72 1.75					

^{*} Standardized to u = 100.

Nephropores only sporadically visible externally; locations from sites of nephridial vesicles: present but location not determinable in 1/2; in c lines in 2/3, 3/4 (?), 4/5 and 5/6 (as Perrier); in b lines in 6/7 (d lines, Perrier); in d lines in 7/8 (d right, and b, left, Perrier); in 8/9, posteriorly, alternating regularly between b and d lines (vice versa, Perrier) (determined as far posteriorly as 25/26; data of Horan, personal communication). Clitellum not visibly developed but dorsal pores faint or absent in 12/13 - 19/20, possibly

indicating a clitellar extent of approximately XIII — XIX; extent noted by Perrier XIII, XIV — XVII. Male genital field: low indistinct male porophores in XVIII in and extending laterally of ab, bearing the male pores in b lines. Accessory genital markings a pair of low suboval tumescences filling ab but mainly presetal in XIX; 3 pairs of circular glandular markings presetal and median to a lines, in XX, XXI and XXII. Female pores not visible (a pair of circular prominences with central pores in a lines of segment X considered by Perrier to be female pores were presumably accessory genital markings as occur in Plutellus manifestus). Spermathceal pores small approximately circular markings, 5 pairs, in 4/5 — 8/9, in b lines.

Septa 4/5 very delicate; 5/6 slightly to moderately thickened; 6/7 — 10/11 strongly and increasingly thickened but never very strong; 11/12 and 12/13 moderately strong; the remainder thin. Septal glands on the pharynx, the last voluminous in IV. Dorsal blood vessel single, continuous onto the pharynx; dorsoventral commissurals in (1V?) V (ventral connections not ascertained), VI - XII; those in VI - IX each with a parietal branch shortly above the junction with the ventral vessel; those in X - XII lacking such branches and forming large latero-oesophageal hearts; each receiving a connective from a harely recognisable supra-oesophageal vessel; this vessel apparently paired in X-X11, a slender filament in IX being apparently its (unpaired?) anterior extension. Nephridia: holonephridia throughout, the first pair of nephridia lying in segment 11. Structure in intestinal segments as follows: from a single, round presental funnel the neck passes posteriorly through the septum to the body of the nephridium in the succeeding segment. The nephridium has a large ectal bladder one face of which is drawn out where it is joined by the narrow terminal duct of the nephridium; between this duct and the neck of the funnel the nephridium forms an intermediate tube which is looped back on itself. The position of the bladder differs according to the position of the nephropore but the length of the terminal duct does not vary; where the bladder discharges in b line the terminal duct is reflexed on itself but is straight where the pore is in d line. In segments preceding the intestine, nephridial structure is similar but the intermediate tube is more coiled, the funnel is extremely small and the neck very narrow. At the hind end nephridia resemble those of the anterior intestinal region and paired coiled organs, seen also in P. manifestus, are present (Horan, personal communication).

Pharynx ending in 11I but covered by the septal glands which extend to the posterior limit of IV in which they conceal the narrow oesophagus. Gizzard in V, strongly fusiform, firm and muscular; moderately large. Calciferous glands 4 pairs, in X — XIII, reniform, with long curved stalks which enter the oesophagus dorsolaterally; each gland subdivided by internal lamellae (observed only in X, XI and XII by Perrier). Intestine commencing in XV; typhlosole absent but dorsal wall of intestine forming a low internal longitudinal ridge. Small testes and large much subdivided iridescent sperm funnels free in X and XI. Seminal vesicles racemose, 2 pairs, in IX and XII (the latter considered to be the sole pair of testes by Perrier). Prostate glands sinuous tubes extending through XVIII and XIX; each with a convoluted muscular duct about one-seventh as long, narrow entally but ectally much widened, straight and at least half the width of the glandular portion; lumen of gland narrow and apparently unbranched. Vasa deferentia? Penial setae absent. Female organs not seen. Spermathecae 5 pairs, discharging anteriorly in

their segments, each a simple narrow pouch, narrowing to about half width ectally to form an indistinctly demarcated duct; each with a long clavate diverticulum with dilated free extremity; the duct of the diverticulum swollen and muscular over about half of its length prior to entering the spermathecal duct. The spermathecae uniform in form and size; length of left spermatheca of IX = 1.05 mm; ratio of length spermatheca: length duct = 4.5; ratio of length spermatheca; length diverticulum = 1.6.

MATERIAL EXAMINED: The type series, consisting of 1 sexual but aclitellate undissected portion here designated the lectotype; 2 posterior ends; 2 intercalary portions and 1 previously dissected portion restricted to the clitellum.

Digaster lumbricoides Perrier, 1872 (Fig. 1 l-K)

Digaster lumbricoides Perrier, 1872, pp. 94-96, pl. 1, fig. 24, pl. IV, fig. 64, 65.
Digaster lumbricoides: Fletcher, 1887, pp. 559-560; 1889, pp. 1531-2; Beddard, 1895, p. 485; Michaelsen, 1900, p. 197; Jamieson, 1970 b, p. 44.

Length 82 mm, w (midclitellar) = 3.3 mm; 158 segments (paralectotype). Form moderately stout, circular in cross section throughout; pigmentless buff in alcohol, clitellum pigmented brick red. Prostomium small, prolobous. First dorsal pore 4/5 (imperforate) with 5/6 perforate (lectotype) or 4/5 (?), 5/6 (imperforate) with 6/7 perforate (paralectotype). Setae small and difficult to discern, in 8 regular longitudinal rows throughout, in 11 posteriorly; ab absent, cd present in the segment bearing the male pores (XVII).

Table 2
Intersetal distances in segment XI in Digaster lumbricoides

	aa		ab		be		ed		dd		dd: u
	mm	st*	mm	st	mm	st	mm	st	mm	st	
lectotype											
paralectotype		8.11	_	3.47		14.51		6.12		43.70	0.44
mean/ab	_	2.34		1.00	_	4.18		1.76	_	12.59	

^{*} Standardized to u = 100.

Nephropores presumably represented by scattered white specks, equatorial and anterior, visible in the clitellar segments. Clitellum annular, strongly protuberant, embracing the posterior 1/3 XII — 1/2 XVII, the posterior limit distinct dorsally hut indefinite ventrally; dorsal pores retained and perforate; setae and intersegmental furrows retained but less distinct than elsewhere. Male pores definite transverse slits in XVII, centred in ab and lying in a common

approximately rectangular tumid field which extends to the equators of segments XVI and XVIII respectively; an approximately oval translucent glandular area located at each corner of the field, in XVI and XVIII, in and lateral of b lines. Female pores anteromedian of scae a of XIII, conspicuous owing to white halos and a common glandular field (lectotype; unrecognizable owing to damage in paralectotype). Spermathecal pores 2 pairs of distinct gaping transverse slits on prominent elliptical papillae in setal rows ab, in 6/7 and 7/8.

INTERNAL ANATOMY. To facilitate comparison with related megascolecoid worms, in which with very few exceptions the spermathecal, female and male pores are one segment behind their locations in *D. lumbricoides*, the segmental enumeration given below has been augmented by an increment of 1.

Septa: 4/5 slightly thickened; 5/6 moderately thickened; 6/7 — 7/8 (lectotype) or 8/9 (paralectotype) strongly and increasingly thickened; 8/9 — 10/11 (lectotype) or 9/10 — 10/11 (paralectotype) moderately strongly thickened; the succeeding septa rapidly decreasing in thickness and becoming delicate. Septal glands on the pharvnx in II — IV, the intervening septa seeming to be present at least centrally. Dorsal blood vessel single, continuous anterior to the brain, which lies in III. Dorsoventral commissural vessels present in V XII, those in VI and VII ramifying on the gizzards but continuing ventrally to join the ventral vessel; those in VIII and IX each with a parietal branch near their junctions with the ventral vessel; those in X — XII forming 3 pairs of latero-oesophageal hearts, each of which receives two connectives, one from the dorsal vessel, the other from the roof of the oesophagus, there being no discrete supra-oesophageal vessel. Nephridia (paralectotype) micromeronephridia throughout the forebody; those in III (II by external segmentation) more numerous and larger than elsewhere and forming transverse aggregations of very many spiral loops which send, on each side, at least two thick composite ducts to the junction of the first and second (external) segments, one duct (the thicker) runs near the pharynx and collects from the majority of the nephridia of this segment; the other is lateral. Micromeronephridia of IV send, on each side, a composite duct anteromedianly to the parietes at approximately the site of the ventral setal couple; by the segment in front of the first gizzard (V) the nephridia have each a separate thin duct running to the anterior border of the segment; by VI they are for the first time purely parietal before this being attached to the posterior septa; by segment VII (the segment of the posterior gizzard) discreteness of the individual nephridia is clearly marked, these being 40 separate exonephric micromeronephridia on each side, attached to the body wall. This condition persists posteriorwards through the forebody and clitellum but the nephridia in X posteriorly become V-shaped, with two major rami. In posterior segments there is a stomate exonephric megameronephridium on each side median to about 8 closed exonephric micromcronephridia; the presental funnels of the former are large. Pharynx ends in IV; in V the o esophagus is dilated to the size of a gizzard but in both specimens its walls are very thin and earry a distinctly developed reticulum of blood vessels; gizzards 2, in VI and VII, large (though neither fills its segment), globose and firm with pronounced museular sheen, the two gizzards separated by a region of unmodified narrow oesophagus anteriorly in VII. Oesophagus narrow and simple to XIII; in XIV and XV swollen and in each segment with a pair of circumferential vessels which join the dorsal vessel; chloragogenous and externally

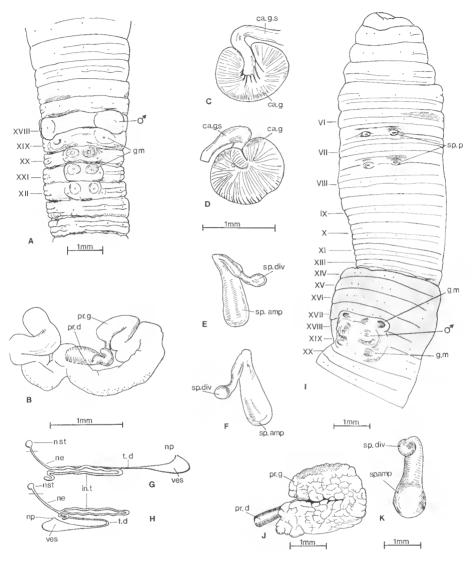


Fig. 1 A-H. — Plutellus heteroporus Perrier, 1873 (lectotype). A, male genital field; B, right prostate gland; C and D, anterior and posterior views of a calciferous gland; E and F, dorsal and ventral views of a spermatheca; G and II, nephridia with bladders discharging in d and b lines respectively.

Fig. 1 I-K. — Digaster lumbricoides Perrier, 1872 (paralectotype). I, forebody, showing male and spermathecal felds; J, right prostate gland; K, ventral view of a spermatheca.

All by camera lucida. Clitellum shaded.

Ca.g. calcifereus gland; ca.g.s, stalk of calciferous gland; g.m., accessory genital marking; in.t., intermediate tubule of nephridium; 3, male pore; ne, neck of nephridium; np, nephropore; nst, nephrostome; pr.d., prostate duct; pr.g., glandular part of prostate; sp.amp, spermathecal ampulla; sp. div, spermathecal diverticulum; sp.p., spermathecal pore; t.d., terminal duct of nephridium; ves, nephridial vesicle.

rugose in XVI; intestine commencing at 1/2 XVII, with a definite oesophageal valve; typhlosole and muscular thickening absent (condition of canal in XV — XVIII not determinable in lectotype owing to previous damage). Small testes and simple funnels free in X and X1; spermatozoal iridescence on the funnel of the lectotype only. Seminal vesicles racemose, in XI and XII, a very large body present in both specimens in XII below the gut and attached to the anterior septum is apparently a much hypertrophied scininal vesicle. Prostate glands each a subrectangular, lobulated, flattened lobe limited to XVIII and with a straight muscular duct running medianwards to its pore; the duct about three fourths the length of the glandular part the ectal portion of which it deeply bisects. Penial setae absent. Female organs not seen. Spermathecae 2 uniform pairs, each with a subspherical ampulla and a wide, longer cylindrical duct, the whole spermatheca with the form of a pouch dilated at its free end; a subspherical sessile diverticulum with spermatozoal (?) sheen joining the anterolateral aspect of the duct immediately before the latter enters the body wall; length of left spermatheca of IX (paralectotype) = 2.2 mm; ratio of length of spermatheca: length duct = 1.6; ratio of length spermatheca: length diverticulum = 5.3.

MATERIAL EXAMINED: 2 clitellate syntypes, one of which had previously been dissected and was in two portions, labelled "Digaster lumbricoides E. P. Nouvelle Hollande, M. J. Verreaux, 1846". The previously dissected specimen is here designated the Icetotype and the other specimen the paralectotype.

Discussion

Plutellus

The new account of *Plutellus heteroporus* considerably augments and largely confirms Perrier's description with which comparisons are drawn. Major divergences are the demonstration of four pairs of calciferous glands, as against three pairs, and location of the gizzard in segment V, not VI as observed by Perrier.

The previously postulated relationship with *Plutellus manifestus*, which has four pairs of calciferous glands of identical and unusual structure and the gizzard in V, is thus confirmed. Similarity of the two species is such as to leave no doubt that they are congeneric and are generically distinct from other species assigned to the genus. Formal restriction of the genus is, however, deferred pending revision and review of the other species. The following common description of the two species comprises a definition of *Plutellus* as it will have to be restricted.

Plutellus s. strict.

Moderately large terrestrial worms (50-150 mm long) with less than 200 segments. Prostomium tanylobous. Dorsal pores commencing at 6/7-8/9. Setae 8 per segment, in regular longitudinal rows, commencing on II; ventral setal couples (ab) wide, dorsal setal couples (cd) much wider and only a little smaller than the intervening distance (bc); dorsal median setal distance (dd)

 $0.24 \cdot 0.26$ of the circumference (u). Nephropores large, first in c lines (on II or III to V or VI); thereafter (VI or VII posteriorly) alternating from d (or slightly below this) to b lines. Clitellum annular, on XIV-XVII or part of XIII also. A pair of combined male and prostatic pores on XVIII in ab; the prostates with thickly tubular tortuous glands and muscular, ectally dilated ducts. Penial setac absent. Accessory genital markings present. Spermathecal pores 4 or 5 pairs, the last at the anterior margin of IX.

Some preclitellar septa strongly thickened. Gizzard strong, in V. Large, paired reniform calciferous glands with very long stalks, 4 pairs, in X-XIII; intestine beginning in XV; typhlosole absent. Supra-oesophageal vessel in 1X, X-XII, XIII. Dorsoventral commissural vessels in V to XII; those in X-XII forming large latero-oesophageal hearts which receive connectives from the supra-oesophageal vessel or from the calciferous vessels, before these join the supra-oesophageal vessel, and from the dorsal vessel. Nephridia stomate holonephridia; the duct of each with a large, elongate, subspherical ectal bladder. Testes and funnels free in X and XI; seminal vesicles in IX and XII. Ovaries and funnels in XIII; ovisacs absent (P. manifestus). Spermathecae discharging anteriorly in their segments; each with a single fairly long clavate diverticulum.

Diagnosis: Holonephric with large nephridial bladders; nephropores in a few anterior segments in c lines, thereafter alternating from d to b lines. Calciferous glands with long stalks present. Combined porcs of a pair of (tubular) prostates and the vasa deferentia in XVIII.

Digaster

The new description of Digaster lumbricoides confirms that it is morphologically very close to the eight known Queensland species of the genus, and that it resembles D. anomala Jamieson, 1970 b, in having the male, female and spermathecal pores dislocated one segment forward. If an increment of 1 be added to the segmental enumeration of these two anomalous species, the morphological homogeneity of the group represented by lumbricoides and the eight Queensland species which is revealed is such as to indicate unequivocally that they must be considered strictly congeneric. A common description of the nine species is as follows:

lumbricoides species-group

Small to very large terrestrial worms (38 mm to more than a metre long). Prostomium zygolobous to tanylobous. Circular in cross section throughout. First dorsal pore in 4/5 or 7/8 (rarely far posterior?). Setae 8 per segment, in straight longitudinal rows throughout; fairly closely paired; cd conspicuously wider than ab; dd: u>0.4 in the forebody. Nephropores scattered, only sporadically visible. Clitellum annular, occupying 4 whole segments and sometimes a part of each adjacent segment, the first segment fully occupied being X1V or rarely X1II. Combined male and prostatic pores a pair on XVIII in a to b lines. Accessory genital markings present or absent. Female pores paired or, rarely, single; anteromedian to setae a of X1V. Spermathecal pores 2 to 3 pairs, intersegmental, the last in 8/9.

Dorsal blood vessel single, continuous onto the pharynx; last hearts in X11 or less commonly XIII; supra-oesophageal vessel present; the hearts in and posterior to X latero-oesophageal; dorsoventral commissurals present anteriorly to the hearts. Subneural vessel absent. Gizzards 2, in V1 and VII, contiguous or separated by unmodified oesophagus. Oesophagus vascular and internally folded and often dilated, in a few to most segments occupied, but extramural calciferous glands absent; intestine commencing in XVIII or rarely (D. lumbricoides) in XVII. Typhlosole and muscular thickening of the intestine absent.

Wholly meronephric; micromeronephridia in anteriormost segments loosely or closely aggregated to form pharyngeal or exonephric tufts; succeeding nephridia exonephric astomate micromeronephridia; in the hindbody the medianmost nephridium on each side possessing a preseptal funnel and usually (and typically) enlarged as an exonephric megameronephridium. Testes and funnels a pair in each of X and X1 or in XI only; testis-sacs absent; seminal vesicles in IX and X11 or in XII only. Prostates one pair, racemose and single or bipartite, the vasa deferentia joining the junction of gland and duct. Ovaries one pair, in X111; ovisacs absent. Spermathecae two or three pairs, with one or two diverticula. All structures sometimes (D. lumbricoides and D. anomala) homeotically displaced one segment forward by suppression of an anterior metamere.

Diagnosis: Gizzards 2 in VI and VII or their homeotic equivalent. Meronephric, with a stomate nephridium median to micromeronephridia on each side of the body in each segment of the posterior region of the body. Combined pores of a pair of (racemose) prostates and the vasa deferentia on XVIII or its homeotic equivalent.

Digaster armifera and D. perrieri, both from the Sydney Basin in New South Wales, comprise a distinct group differentiated from the lumbricoides group by location of the gizzards in V and VI (without homeosis) and the possession of penial setae. Median stomate megameronephridia have been demonstrated in posterior segments (Jamieson, 1970 b) in D. armifera but have yet to be recorded for D. perrieri. At present these must be retained in Digaster but it seems possible that they may have replicated the gizzard independently of the lumbricoides group.

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Synopsis

Plutellus heteroporus, the type-species of a genus which has a circummundane distribution and contains over one hundred known species, is shown to be morphologically close to only P. manifestus from New South Wales. Evidence is presented for restricting the genus to these two species though this step is deferred pending revision of Plutellus s. lat.

Digaster lumbricoides, the type-species of its genus, is shown to have the metameric abnormality previously shown for Digaster anomala and to be representative of a group of 9 species from Queensland and northern New South Walcs. The affinity of the remaining species of the genus with this lumbricoides species-group is discussed. Presence of median stomate nephridia, in addition to elosed micromeronephridia, indicates that Digaster is assignable to a Dichogaster-Megascolides group of genera and that affinities with Megascolex are less close than was previously considered.

Résumé

Description des types des genres de Lombriciens Plutellus et Digaster (Megascolecidae : Oligochaeta)

L'auteur démontre que *Plutellus heteroporus*, espèce-type d'un genre eosmopolite eomprenant plus de cent espèces, n'est morphologiquement proche que de la seule espèce *P. manifestus* en provenance de la Nouvelle-Galles du Sud. Il conviendrait donc de restreindre le genre à ces deux espèces, tout au moins jusqu'à ce que la révision complète du genre *Plutellus* s. lat. ait été effectuée.

Digaster lumbricoides, espèce-type du genre, présente l'anomalie métamérique déjà observée ehez D. anomala et se trouve être représentatif d'un groupe de neuf espèces en provenance du Queensland et du nord de la Nouvelle-Galles du Sud. Les affinités des autres espèces du genre avec ee groupe d'espèces lumbricoides sont discutées.

La présence de néphridie médiane avec pavillon, en plus de microméronéphridies sans pavillon, permet de rattacher *Digaster* au groupe de genres *Dichogaster-Megascolides*, et de penser que ses affinités avec *Megascolex* sont moins grandes qu'on ne l'avait eru jusqu'à maintenant.

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